

## THE SOUTHERN AUSTRALIAN SPECIES OF *SPYRIDIA* (CERAMIAEAE: RHODOPHYTA)

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### Summary

WOMERSLEY, H. B. S., & CARTLEDGE, Sally A. (1975).—The southern Australian species of *Spyridia* (Ceramiaeae: Rhodophyta), *Trans. R. Soc. S. Aust.* **99**(4), 221-233, 30 November, 1975.

Four species of *Spyridia* are recognised on southern Australian coasts. *S. filamentosa* (Wulfen) Harvey (including *S. biannulata* J. Agardh, *S. breviararticulata* J. Agardh, and *S. spinella* Sonder) is common in sheltered to moderately rough water. *S. dasyoides* Sonder (including *S. opposita* Harvey and *S. prolifera* Harvey) is fairly common on rough-water reefs and in deeper water. *S. squalida* J. Agardh (including *S. wilsonis* J. Agardh) is a less common, usually deep-water, species. *S. tasmanica* (Kuetzing) J. Agardh occurs in relatively calm localities but where there is often a strong current. The Australian species differ in vegetative aspects such as arrangement and diameter of the ramelli, but agree well in the development of the thallus and reproductive structures, and emphasize the generic uniformity of the species ascribed to *Spyridia*.

### Introduction

While *Spyridia* is a distinctive and easily recognised genus of the Ceramiaeae, the taxonomy of the southern Australian species has been confused. Some 10 species have been credited to the region, but the only recent account of the species by Lucas & Perrin (1947) and a key by May (1965) offer little help in recognising or separating the species.

The type species of *Spyridia*, *S. filamentosa* (Wulfen) Harvey, has recently been described in detail by Hommersand (1963, p. 177), who reviewed earlier studies and clarified its vegetative and reproductive features. Indian material of this species has been studied by Krishnamurthy (1968). Other species referred to *Spyridia* agree well with the type in general morphology, presence of nodal and internodal cell bands, branches of limited growth (ramelli or "brachyblasts") and unlimited growth, and in reproductive features. However, the features which Hommersand (1963, p. 177) used to distinguish *S. filamentosa* from other species of *Spyridia* do not apply satisfactorily to the Australian species. Cortication by tiers of nodal

and internodal cells is found in all species (the cell shape varies considerably in *S. filamentosa*), and all species have radially disposed ramelli (opposite in *S. dasyoides*) which (except *S. squalida*) commonly have mucronate end cells.

Growth of the uniaxial thallus is from an apical cell which cuts off a row of short axial cells which develop into a branch of unlimited growth, from each cell of which one or more ramelli develop laterally. The ramelli are of limited growth, developing rapidly to between 10 and 30 cells long by divisions of their apical cell, and following cessation of cell division they expand by cell elongation to their mature length of generally 1-3 mm. The axial cells also cut off in alternating sequence a ring of periaxial<sup>†</sup> cells, which form a band around the node between two axial cells. Each of these periaxial (nodal) cells cuts off two cells from its lower end, and these elongate and become attached by pit-connections to the nodal cells of the next lower segment. Thus the thallus shows bands of shorter and broader nodal cells alternating with the bands of internodal cells,

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<sup>†</sup> This term is used for cells cut off from, but of different form to, an axial cell. Cells of similar form to the axial cell, as found in the polysiphonous families of the Ceramiales, are still referred to as pericentral cells.

which are longer, narrower, and approximately twice as many as the nodal cells. Further cortication occurs some distance from the branch apices, from descending rhizoidal cells developed from the nodal cells, and this obscures the regular pattern of nodal and internodal cell bands, especially in certain species (e.g. *S. squalida*).

The cells of the ramelli each cut off a ring of 6-8 cells from their upper end, and these develop into a nodal band 1-3 cells broad in *S. filamentosa*. *Spyridia* is readily recognised by the alternating nodal and internodal bands, and ramelli with corticated nodes.

Reproductively *Spyridia* is also distinctive, especially in that the carposporophyte becomes surrounded by pericarpic filaments developed from the segments above and below the one bearing the procarp. These filaments can give the appearance of a cystocarp with a well developed pericarp wall, being held together by a mucilaginous sheath and some lateral pit-connections, but they disintegrate fairly readily in preserved material.

Procarps (3-6) are produced on small lateral branchlets of restricted growth. According to Hommersand (1963, p. 191), three pericentral (periaxial) cells are normally formed in each fertile segment, one of which (the supporting cell) bears the carpogonial branch, and each pericentral forms an auxiliary cell. Hommersand reported that the carpogonium fuses with the third cell of the carpogonial branch which then connects with the auxiliary cells by means of connecting cells. Thus two (or rarely three) gonimoblasts are initiated and the mature cystocarp is commonly bilobed. Krishnamurthy (1968, p. 48), however, observed only two pericentral cells per fertile segment in material from South India, and considered that the fertilised carpogonium divided into two cells, each of which fused with an auxiliary cell.

Spermatangia cover several cells in the lower part of the ramelli, usually excluding the basal cell. They are derived from filaments originating from the nodal cells, which grow over the two adjacent cells, then cut off spermatangial mother cells before forming the continuous surface layer of spermatangia.

Tetrasporangia occur on the lower cells of the ramelli, being sessile and mostly on the upper (adaxial) side. Hommersand (1968, p. 196) considers that they arise directly as protrusions from the axial cell, while Krishnamurthy (1968, p. 47) considers that they are formed from periaxial cells.

Some 10 species of *Spyridia* have been recorded from southern Australia. This study recognises only four species, including *S. filamentosa*. The thallus development and morphology, and the structure of reproductive organs, are very similar to those of *S. filamentosa*, and the Australian species differ mainly in vegetative features. The descriptions below are therefore confined largely to recognition of the species, with brief notes only on reproductive details.

#### Key to southern Australian species

1. Ramelli robust, opposite and decussate, usually 100-150  $\mu$ m thick with isodiametric cells and nodal bands 3-5 cells broad ..... *S. dasyoides* (p. 231)
1. Ramelli slender, single or whorled but not opposite, less than 70  $\mu$ m thick, usually with cells longer than broad, and nodal bands 1-3 cells broad ..... 2
2. Ultimate branchlets stout (1-1 mm thick), markedly basally constricted, heavily corticated to their apices, bearing slender, irregularly branched ramelli ..... *S. squalida* (p. 229)
2. Ultimate branchlets slender (under 1 mm thick), not or only slightly basally constricted, cortication only on older branches, with ramelli either one per segment or verticillate ..... 3
3. Ramelli one per segment, 35-65  $\mu$ m thick, nodal bands 2-3 cells broad ..... *S. filamentosa* (p. 222)
3. Ramelli becoming verticillate (1-6), 20-40  $\mu$ m thick, nodal bands 1 cell broad ..... *S. tasmanica* (p. 227)

***Spyridia filamentosa* (Wulfen) Harvey 1833:** 336; 1844: 449; 1846, pl. 46; 1855a: 557; 1859: 329; 1863, synop.: 42. J. Agardh 1852: 340; 1876: 268; 1897: 13. Boergesen 1917: 223, figs 222-226. Feldmann-Mazoyer 1940: 348. Guiler 1952: 98. Hommersand 1963: 177, figs 4-10. Hooker & Harvey 1847: 409. Krishnamurthy 1968: 42. Newton 1931: 394, fig. 236. Okamura 1932: 130. Reinhold 1897: 60. Sonder 1853: 680; 1880: 16. Tate

Fig. 1. *Spyridia filamentosa*. A. Pt Stanvac, S. Aust. (Lewis, 14.iv.1972; ADU, A41869). B. Female plant with young cystocarp (Pt Denison, W. Aust. Kraft, 14.xii.1971; ADU, A41175). C. Male plant with spermatangial ramelli (Aldinga, S. Aust. Cartledge, 30.iii.1972; ADU, A41815). D. Tetrasporangial plant (A41815).

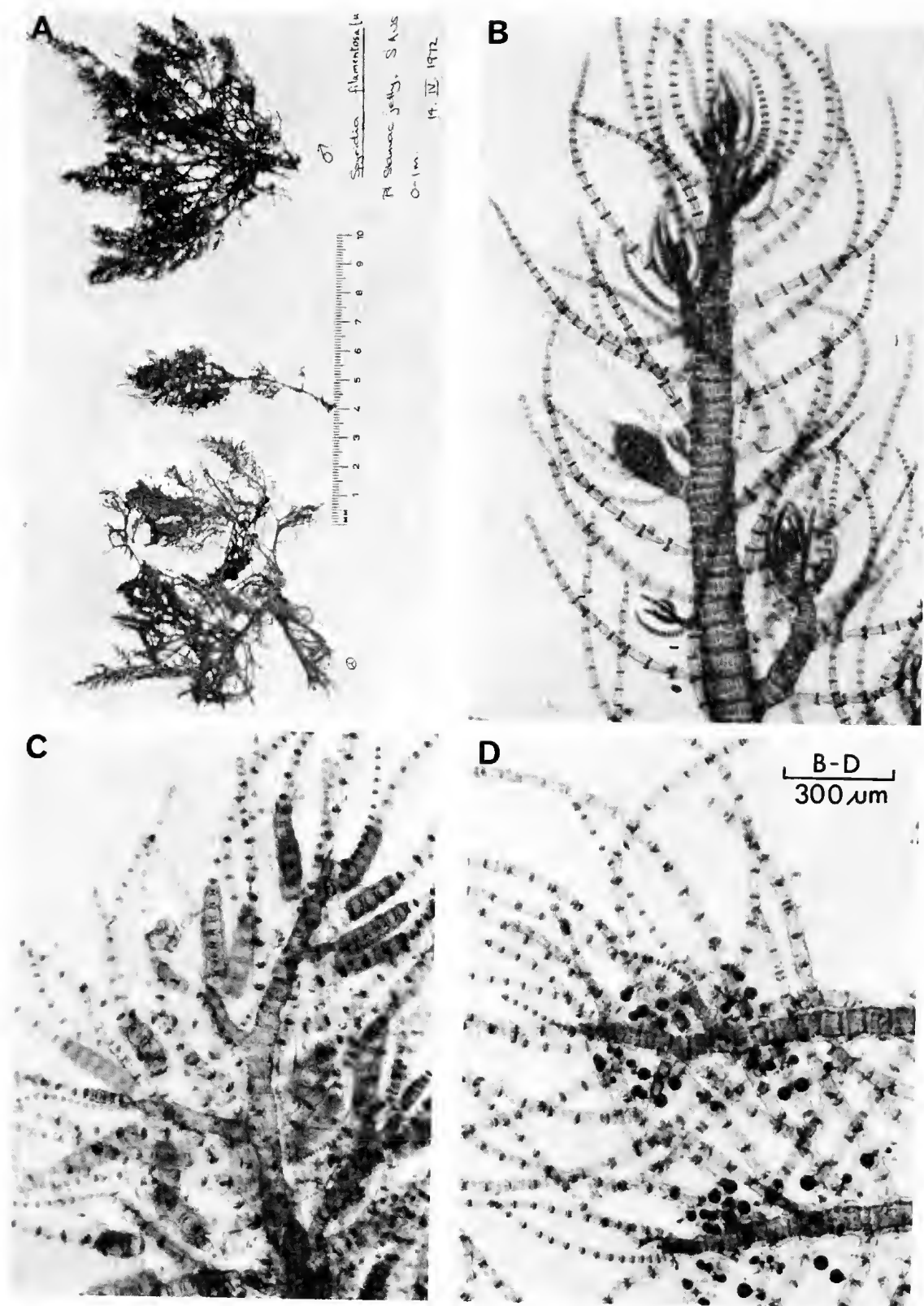


Fig. 1.



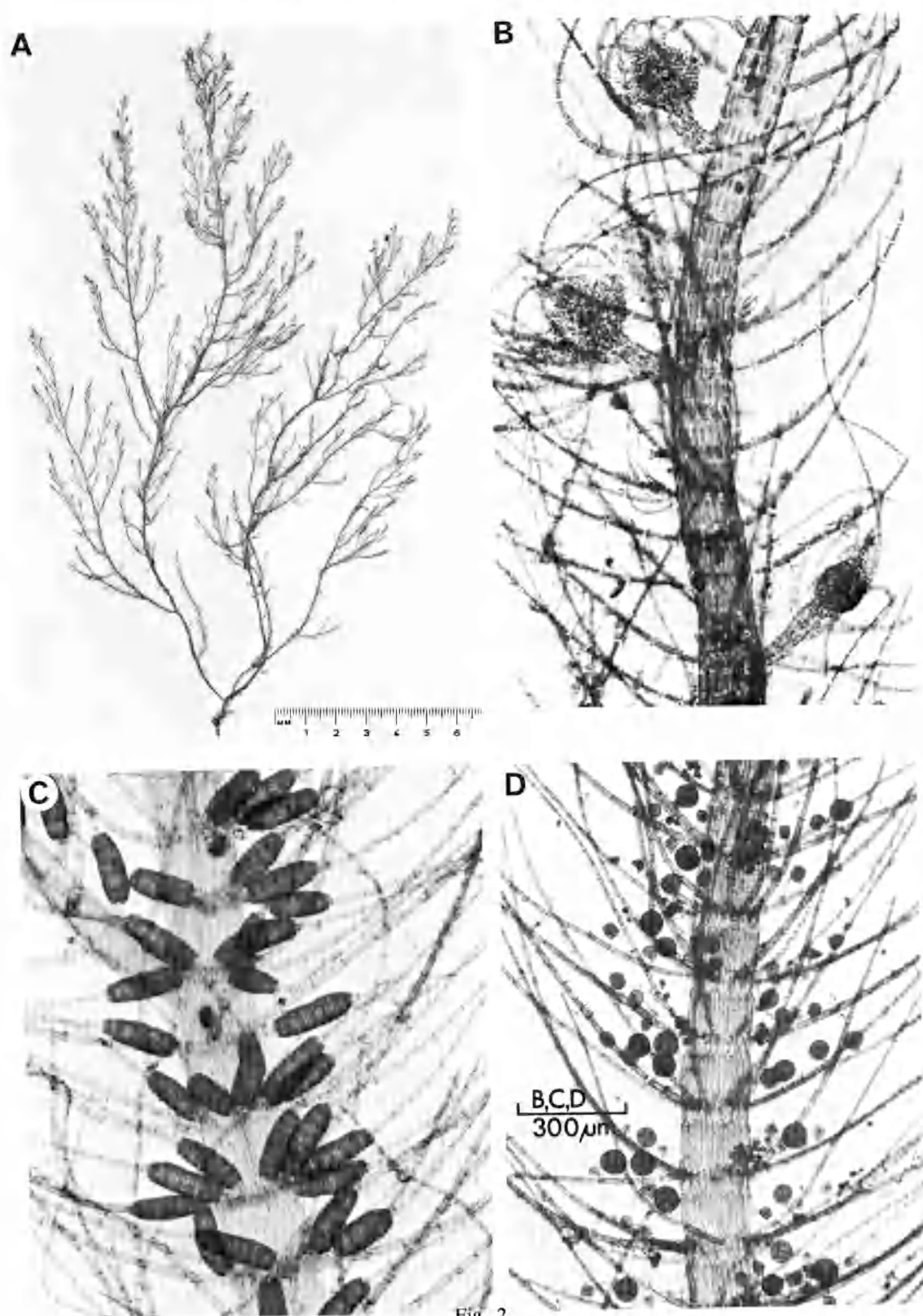


Fig. 2.

1882: 18. Tisdall 1898: 505. Wilson 1892: 181. Womersley 1958: 157.

*Fucus filamentosus* Wulfen 1803: 64.

*S. filamentosa* var. *arbuscula* Sonder 1855: 518.

*S. biannulata* J. Agardh 1876: 267; 1897: 13.

De Toni 1903: 1426. Guiler 1952: 98. Lucas

1909: 52; 1929a: 25; 1929b: 53. Lucas & Perrin

1947: 363. May 1965: 369. Okamura 1932:

130. Reinhold 1897: 60; 1899: 50. Sonder 1880:

16. Tisdall 1898: 505. Wilson 1892: 181.

Womersley 1950: 180.

*S. breviaristulata* J. Agardh 1876: 268; 1897:

13. De Toni 1903: 1427. Guiler 1952: 98.

Lucas 1909: 52; 1929a: 25; 1929b: 53. Lucas &

Perrin 1947: 363. May 1965: 369. Okamura

1932: 130. Reinhold 1897: 60; 1899: 50. Sonder

1880: 16.

*S. spinella* Sonder 1845: 53; 1846: 168; 1880:

16. J. Agardh 1852: 342; 1876: 269; 1897: 13.

De Toni 1903: 1430. Harvey 1863, synop.: 42.

Kuetzing 1849: 668; 1862: 16, pl. 51c,d. Lucas

1909: 52. May 1965: 369. Mazza 1925, no. 824.

Okamura 1932: 130.

#### FIGS 1, 3A, B

*Thallus* (Fig. 1A) usually 7–18 cm high, epilithic or epiphytic on various larger algae and seagrasses, lax and soft, irregularly much branched on all sides with longer and shorter branches intermixed, with one to several axes (often poorly defined) from an originally discoid holdfast, soon becoming fibrous or stoloniferous and entangled, commonly grey to grey-red, sometimes red-brown, in colour. Axes and larger branches corticated, terete; axes  $\frac{1}{2}$ –1 (–1½) mm thick, tapering to branches 300–500  $\mu$ m thick and branchlets 100–300  $\mu$ m thick; laterals arising from periaxial cells or adventitiously from cortical cells. Segments usually clearly defined on branchlets (Fig. 1B), variable in length and proportions but usually  $\frac{1}{2}$ –1 times as long as broad, with bands of shorter nodal cells and longer internodal cells alternating; nodes with 11–14 periaxial cells, each corresponding to two internodal cells except for the (usually) larger periaxial cell bearing the ramellus. Cortication usually commencing a few mm from the apices but very variable, consisting of rhizoidal cells lying between the internodal cells and gradually forming a continuous cortex 1(–2) cells thick. Ramelli (Figs 1B, 3A, B) single per segment, irregularly spirally arranged,  $\frac{1}{2}$ –1½ mm long with 12–20(–27) cells, linear or gently tapering apart from the terminal 2–3 very short

cells (Fig. 3A) which taper abruptly to a mucronate cell, (35–)40–55(–65)  $\mu$ m thick with cells (1½–)1½–2½(–3) times as long as broad; mucronate end cell often lost from older ramelli, ramelli with about 9 nodal cells, each usually cutting off 1(–2) cells anteriorly, giving a nodal band 2–3 cells broad.

*Cystocarps* (Fig. 1B) short-stalked, usually bilobed, lobes globular, 300–700  $\mu$ m across.

*Spermatangia* covering the lower (except basal) several segments of ramelli (Fig. 1C), forming male organs 75–120  $\mu$ m in diameter.

*Tetrasporangia* (Fig. 1D) sessile, 1–3 per cell on lower cells of ramelli, mostly on the upper (adaxial) side, spherical, 50–75  $\mu$ m in diameter, tetrahedrally divided.

*Type locality*: Adriatic Sea.

*Type*: ?

*Distribution*: All around the Australian coast (including Tasmania) in conditions of moderate to slight water movement.

*Spyridia filamentosa* is recognised as a widely distributed species, having been recorded from most seas, and many authors (e.g. Harvey 1846, pl. 46; Feldmann-Mazoyer 1940, p. 348) refer to it as a very variable species. J. Agardh (1876, p. 268) in segregating two Australian species (*S. biannulata* and *S. breviaristulata*) from *S. filamentosa*, referred to their similarity in habit with *S. filamentosa* and the large number of forms classed as this species. J. Agardh apparently regarded his two segregate species with some doubt, and a detailed study of extensive collections of Australian material does not provide any satisfactory way of segregating *S. biannulata* and *S. breviaristulata* from *S. filamentosa*.

The type of *S. biannulata* is from Tasmania (Georgetown, Tas., Gunn, LD, 51300, selected as lectotype) and was distinguished by J. Agardh in having more conspicuous bands of nodal and internodal cells and being less corticated above. *S. breviaristulata* is based on specimens from Whitsunday I., Queensland (lectotype in LD, 51311), and was distinguished by having the nodal and internodal bands short and of almost equal length. The variation in *S. filamentosa* encompasses the above features of both *S. biannulata* and *S. breviaristulata*.

Fig. 2. *Spyridia tasmanica*. A. Portarlington, Vic. (Wollaston, 17.viii.1956; ADU, A20567). B. Female plant with young cystocarps (Investigator Strait, S. Aust., 33 m deep, Watson, 24.i.1971; ADU, A41066). C. Male plant with spermatangial ramelli (Tapley Shoal, S. Aust., 15 m deep, Shephard, 2.ii.1969; ADU, A33538). D. Tetrasporangial plant (A41066).

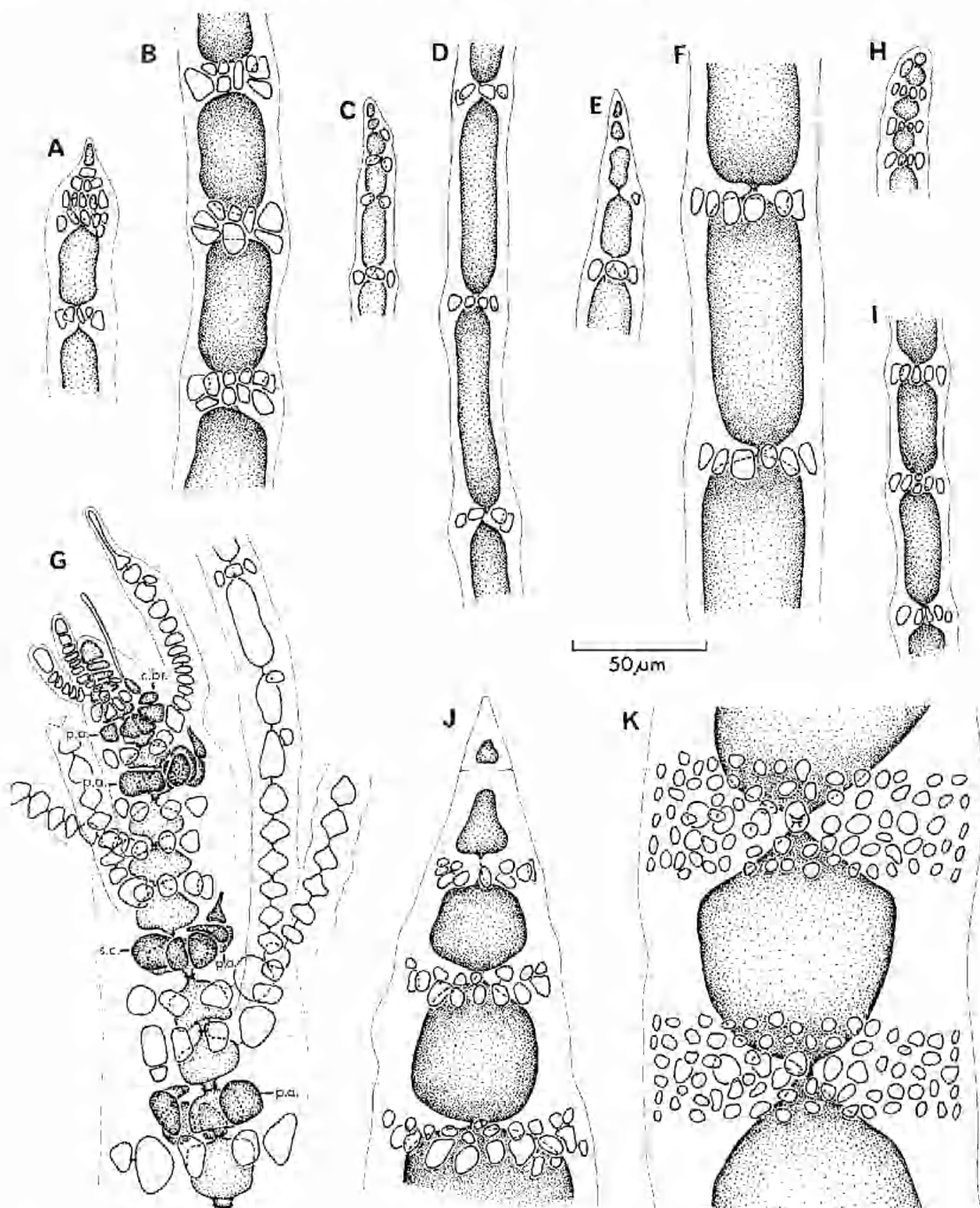


Fig. 3. A, B. *S. filamentosa*. Apex and mid region of ramellus, with periaxial cells in face view (A41815).  
 C, D. *S. tasmanica*. Ditto (A41066).  
 E, F. *S. tasmanica*. Ditto, robust form (A37622).  
 G. *S. tasmanica*. Female axis with procarys. (Gt Taylor Bay, Bruny I., Tas., 10 m deep. Shepherd, 7.ii.1970; ADU, A35287). c.br.—carpogonial branch; p.a.—periaxial cell; s.c.—supporting cell.  
 H, I. *S. squalida*. Apex and mid region of ramellus, with periaxial cells in face view (A26375).  
 J, K. *S. dasyoides*. Ditto (A20170).

*S. filamentosa* var. *arbuscula* Sonder (1855, p. 518) from Wilsons Promontory, Vic., May 1853 (type in MEL, 45181) is typical of the species and not a distinct variety.

*S. spinella* Sonder (type in MEL, 502090) was based on Preiss material from Western Australia. The type has somewhat broader and stouter ramelli than most specimens of *S. filamentosa*, with cells about as long as broad and the nodal bands of the ramelli 2–3 cells broad. Collections from Cottesloe, W. Aust., reef pools (Parsons, 14.xi.1968; ADU, A34072) and from Elliston, S. Aust. (Womersley, 15.i.1951; ADU, A15142) agree well with the type in having densely aggregated ramelli 400–800  $\mu\text{m}$  long, composed of 15–18 cells, 50–65(–90)  $\mu\text{m}$  thick and 1–1½ times as long as wide. This is within the extremes of *S. filamentosa* and is probably typical of plants occurring in rock pools subject to moderate to considerable water movement. These plants are much closer to typical *S. filamentosa* than the Brest specimen discussed below, and are provisionally placed under *S. filamentosa*, but further studies on this "spinella" form and its variation are desirable.

*S. filamentosa* has been studied by several authors, most recently by Feldmann-Mazoyer (1940, p. 348), Hommersand (1963, p. 183) and Krishnamurthy (1968, p. 42). The Australian material agrees well with these descriptions, and also with material from Leghorn, Italy (Sartoni, 18.viii.1973; ADU, A43938). However, material from Brest, France (Cabioc'h, Dec. 1972; ADU, A43050) has distinctly more robust ramelli (about 100  $\mu\text{m}$  thick, cells scarcely longer than wide) which have 2–3 very small basal cells with the parent periaxial cell not enlarged, in contrast to the full-sized basal cells and enlarged periaxial cell of typical *S. filamentosa*. These two collections indicate that there may be greater variability in European *S. filamentosa* than in the Australian material.

Hommersand (1963) and Krishnamurthy (1968) differ in some details in their accounts of reproduction in the material they studied, as mentioned above in the introduction. Australian material (e.g. Aldinga, S. Aust. Cartledge, 30.iii.1972; ADU, A41881) shows three periaxial cells in fertile segments, but clarification of immediate post fertilisation stages has not been possible. No clear stages have been observed of a tetrasporangium arising directly from the axial cell of a ramellus (Hommersand 1963, p. 194), but it appears more likely that

periaxial cells are usually transformed into tetrasporangia. The number of periaxial cells in a ramellus does vary slightly, so it is not possible to state as Hommersand does that tetrasporangia must arise directly from the axial cell because the number of periaxial cells is the same in sterile or fertile segments.

***Spyridia tasmanica* (Kuetzing) J. Agardh 1852:**  
342. Gordon 1972: 39. Harvey 1859:  
329. Kuetzing 1862: 14, pl. 42 c, d.  
Sonder 1853: 680.

*S. filamentosa* var. *tasmanica* Kuetzing 1849: 666.

*S. filamentosa* var. *verticillata* Harvey 1844: 449.

*Wrangellia setigera* Harvey 1859: 309, pl. 191A; 1863, synop.: 27. J. Agardh 1876: 622; 1879: pl. 32, fig. 3. De Toni 1897: 133; 1924: 149. Gordon 1972: 39. Guiler 1952: 99. Lucas 1909: 23; 1929a: 16. May 1965: 365. Mazza 1919, no. 678. Okamura 1932: 133. Sonder 1880: 29. Tisdall 1898: 511. Wilson 1892: 170.

#### FIGS 2, 3C-G, 4A-C

*Thallus* (Fig. 2A) usually 8–25 cm high, irregularly much branched, epilithic or on *Amphibolis*, with a small, discoid holdfast, grey-red to red-brown in colour. Branching irregularly alternate, branches terete, with one to a few main axes and prominent lateral branches, bearing lesser branches and branchlets on all sides, with whorled ramelli. Axes 1–1½(–2) mm thick, branches about ½ mm thick, lesser branchlets 200–400  $\mu\text{m}$  thick. Segments (½–)¾–1½ times as long as broad (Fig. 2D), with usually 12 periaxial cells, each producing two internodal cells; cortication by rhizoidal cells from the nodal cells, commencing within 1–2 cm of apices and becoming heavy on axes and main branches. Ramelli (Figs 2D, 3C–F) 1(–3) per node near apices, becoming whorled (3–6(–8) per whorl with the addition of adventitious ramelli), arising from enlarged periaxial cells, ¾–2 (–3) mm long with 20–30 (–35) cells of greatest diameter (15–)20–35 (–40)  $\mu\text{m}$  and 3–5 times as long as broad, the end cell mucronate; robust form with ramelli (12–)15–20 cells long, greatest diameter 30–40(–45)  $\mu\text{m}$  and 1½–2½ times as long as broad. Ramelli with a single row of 8–14 nodal cells (Fig. 3D, F).

*Cystocarps* (Figs 2B, 4A) terminal on a short branchlet bearing ramelli, ¼–¾ mm in diameter.

*Spermatangia* cover 2–6 cells (Figs 2C, 4B) within 1–2 cells of base of ramellus, forming a cylindrical male organ 70–130  $\mu\text{m}$  in diameter and 1–6 times as long as broad.



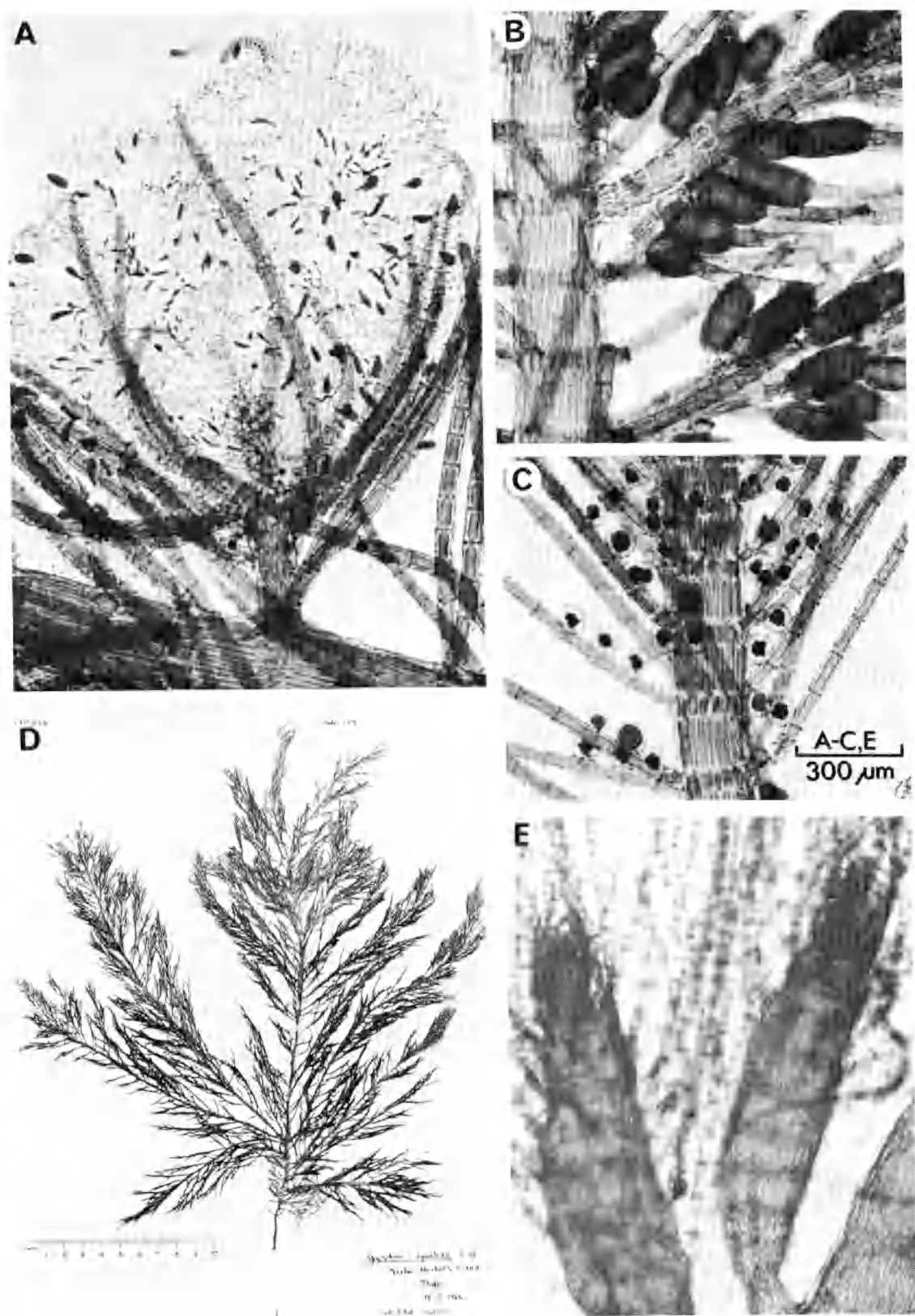


Fig. 4.



*Tetrasporangia* (Figs 2D, 4C) on 1–4 cells near the base of the ramelli, borne mostly on the upper (adaxial) side, 60–100(–120)  $\mu$ m in diameter when mature, tetrahedrally divided.

*Type locality*: Tasmania (probably Gunn, ex Hooker).

*Type*: L (941, 311...371).

*Distribution*: From Elliston, S. Aust. to Western Port, Vic. and around Tasmania. Generally in relatively calm localities, often with considerable current, 2–35 m deep, occasionally in partly sheltered habitats and shaded rock pools on rough-water coasts.

Development of reproductive structures in *S. tasmanica* appears to be very similar to that in *S. filamentosa*. The female axes (Fig. 3G) arise as short laterals and bear up to 5 procarys, separated by one or two sterile segments each with eight periaxial cells, one of which bears a ramellus. Each procary consists of 3 (rarely 4) periaxial cells, one of which is the supporting cell bearing the 4-celled carpogonial branch. Immediate post-fertilisation stages have not been clearly followed, but usually two groups of gonimoblast cells develop, probably from fusion cells originating from auxiliary cells cut off from the supporting cell and one of the other fertile periaxial cells. Sterile pericarp filaments arise from the periaxial cells of segments above and below the procary-bearing segment, forming a cystocarp similar to that in *S. filamentosa*.

Development of spermatangia and tetrasporangia is similar to that in *S. filamentosa*.

*S. tasmanica* is a distinctive species with its whorled ramelli and single row of nodal cells. The ramelli are typically slender (20–35  $\mu$ m thick), with mature cells 3–5 times as long as broad. However, some plants from rougher-water localities [e.g. Elliston, S. Aust., 7 m deep (Shepherd, 20.x.1970; ADU, A37622) and Cape Lannes, S. Aust., in shaded pool (Kraft, 12.ii.1972; ADU, A41809)] have more robust ramelli, 30–40(–45)  $\mu$ m thick (Figs 3E, F, 4B, C) and mature cells 1½–2½ times as long as broad. Otherwise the latter specimens are similar to the majority of plants, and the type, of *S. tasmanica*, and the more robust, shorter-celled ramelli are regarded as

more characteristic of plants found under rougher-water conditions. Further studies on this form are, however, desirable.

*Spyridia squalida* J. Agardh 1876: 270; 1897: 16. De Toni 1903: 1436. Lucas 1909: 52; 1929b: 53. Lucas & Perrin 1947: 364. May 1965: 369. Okamura 1932: 130. Reinbold 1897: 60. Sonder 1880: 16. Tate 1882: 18.

*S. wilsonis* J. Agardh 1897: 16. De Toni 1903: 1435. Lucas 1909: 52. Lucas & Perrin 1947: 364. May 1965: 396. Okamura 1932: 130. *S. valida* Sonder 1880: 16 (nomen nudum).

#### FIGS 3H, I, 4D, E

*Thallus* (Fig. 4D) usually 10–30 cm high, robust, erect, irregularly and proliferously branched, epilithic with one to several axes from a small discoid holdfast, usually with long, much branched, laterals on all sides, grey-red to red-brown in colour and when dried often appearing somewhat farinaceous. All branches terete and corticated to their apices, axes and main branches linear, branchlets (Fig. 4E) basally constricted and bearing densely arranged ramelli, especially on their upper parts, sometimes denuded below. Axes 1½–2½ mm thick, denuded below or with short, proliferous branchlets, tapering slightly to branches 1–1½ mm thick and lesser branchlets ½–1 mm thick. Segments largely obscured by cortication, ½–⅓ as long as broad, with 16 periaxial cells and about twice as many internodal cells; cortication commencing within a few axial cells of apices, pseudo-parenchymatous, 2–3 cells thick on branchlets, several cells thick on axes. Ramelli (Figs 3H, I, 4E) one per segment close to apices and derived from periaxial cells, but scattered adventitious ramelli (usually) densely cover the branchlets, sometimes persisting onto larger branchlets; ramelli ½–1(–1½) mm long with (10–)14–20(–24) cells of greatest diameter (20–)30–40(–45)  $\mu$ m and (1–)1½–2(–2½) times as long as broad. Ramelli with a single row of small nodal cells (Fig. 3I) derived from 5–6 periaxial cells each of which cuts off 2–3 outer cells in the same transverse plane.

*Cystocarps* short-stalked, globular-bilobed, ½–¾ mm in diameter.

Fig. 4. *Spyridia tasmanica* (robust form). A. Female plant with squashed mature cystocarp (Elliston, S. Aust., 7 m deep in bay. Shepherd, 20.x.1970; ADU, A37622). B. Male plant with spermatangial ramelli (A37622). C. Tetrasporangial plant (A37622). *Spyridia squalida*. D. Victor Harbor, S. Aust. (Womersley, 18.iii.1966; ADU, A30032). E. Branchlets and ramelli (Pt Elliot, S. Aust. Dodd, 12.iii.1963; ADU, A26375).

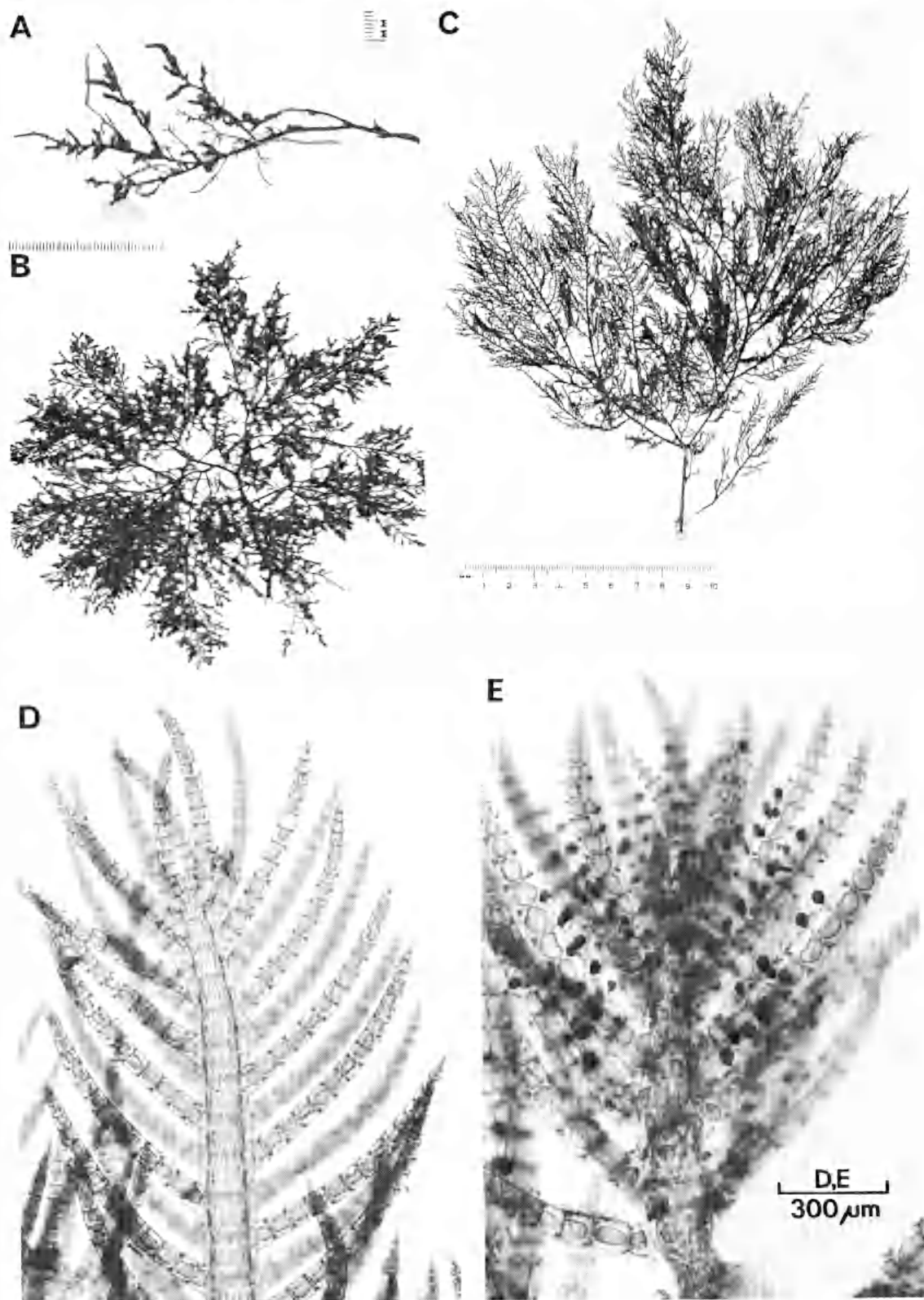


Fig. 5.

*Spermatangia* cover the lower 2-6 cells (except basal cell) of ramelli, forming a male organ 50-80  $\mu$ m in diameter.

*Tetrasporangia* borne on the lower several cells of the ramelli, largely on the upper (adaxial) side, 1(-2) per cell, sessile, spherical to slightly ovoid, 40-60  $\mu$ m in diameter when mature, tetrahedrally to sub-crucially divided.

*Type locality*: "Nov. Holland. australem".

*Type*: Herb. Agardh, LD, 51533.

*Distribution*: From Geographe Bay, W. Aust. to Waratah Bay, S. Gippsland, Vic., usually in deep water (2-24 m deep).

Female axes of *S. squalida* develop as short, adventitious branchlets which are more heavily corticated than in other species but less so than in vegetative branchlets of this species. Alternating segments each bear a procarp, with the sterile segments bearing ramelli. Usually three periaxial cells occur in fertile segments, one (the supporting cell) producing a 4-celled carpogonial branch. Two, or probably often 3, auxiliary cells are formed, leading to a carposporophyte with two or three lobes. The pericarp develops similarly to that in other species.

*S. squalida* is a distinctive and robust species of *Spyridia*, having cortication to the apices and thus forming swollen, basally-constricted, branchlets, bearing ramelli often densely scattered but usually soon denuded. The farinaceous appearance is also a common feature of older, dried plants.

*S. wilsonii* J. Agardh is typical *S. squalida*. The type of the former is from Pt Phillip Hds, Vic. (J. B. Wilson, 1887: LD 51532), and the thallus is not compressed as stated by J. Agardh (1897) and May (1965).

*S. valida* Sonder (1880: 16) is a nomen nudum, based on a specimen in MEL (45195) from Geographe Bay, W. Aust. (Bunbury, 1875), accompanied by Sonder's drawings. It is typical *S. squalida*.

*S. squalida* was recorded from Port Alfred (Kowie), South Africa by Barton (1896, p. 196), and the record repeated by De Toni (1903, p. 1436) and Lucas & Perrin (1947, p. 364). This record almost certainly applies to some other species, probably to *S. plumosa* Schmitz ex J. Agardh (G. F. Papenfuss, pers. comm.).

*Spyridia dasyoides* Sonder 1853: 680; 1880: 16. J. Agardh 1876: 272. De Toni 1903: 1437. Harvey 1863, synop.: 42. Lucas 1909: 52. Lucas & Perrin 1947: 364. May 1965: 369. Okamura 1932: 130. Tate 1882: 18. Tisdall 1898: 505.

*S. opposita* Harvey 1855b: 256; 1860: pl. 158. Adams 1972: 83. J. Agardh 1876: 270; 1897: 14. De Toni 1903: 1431; 1924: 502. Guiler 1952: 98. Lucas 1909: 52; 1929a: 25; 1929b: 53. Lucas & Perrin 1947: 363, fig. 182. May 1965: 369. Mazza 1912, no. 421. Okamura 1932: 130. Reinhold 1897: 60. Shepherd & Womersley 1970: 135. Sonder 1880: 16. Tate 1882: 18. Tisdall 1898: 505. Wilson 1892: 181. Womersley 1950: 180; 1966: 151.

*S. prolifera* Harvey 1863: pl. 274. J. Agardh 1876: 269; 1897: 14. De Toni 1903: 1431. Lucas 1909: 52. Lucas & Perrin 1947: 362, fig. 181. May 1965: 369. Mazza 1912, no. 422. Sonder 1880: 16.

### FIGS 3J, K, 5

*Thallus* (Fig. 5A-C) usually 10-20 cm high, erect, epilithic or epiphytic, much branched with one to several axes from an originally discoid holdfast which soon becomes fibrous and stoloniferous, dark red to red-brown in colour. Axes and larger branches heavily corticated, terete to angular and becoming four-sided with thickened cortical flanges in line with the 4 ranks of ramelli, densely branched. *Axes* 1-2 (-2½) mm thick, often denuded but sometimes with numerous, short, proliferous branchlets, tapering to branches ½-¾ mm thick and lesser branchlets ¼-½ mm thick; branching usually subdistichous (Fig. 5C) with laterals arising from nodal cells. *Segments* largely obscured by cortication, ½-1 times as long as broad, with 8 periaxial cells producing 16 internodal cells and the 8 cells soon with interposed rhizoidal cells giving both nodal and internodal rings of 16 cells (Fig. 5D); cortication commencing within a few segments of apices, of elongate cells later appearing pseudo-parenchymatous, a few cells thick on branchlets, many (especially on flanges) cells thick on axes. *Ramelli* (Figs 3J, K, 5D, E) arising from an enlarged periaxial cell, in opposite and more or less decussate pairs (Fig. 5D) on successive segments (often displaced to two rows on each side in the plane of branching), (1-)1½-2(-2½) mm long with (16-)18-22 cells, relatively uniform

Fig. 5. *Spyridia dasyoides*. A. Holotype (MEL, 45128). B. Robe, S. Aust. (Cartledge, 14.v.1972; ADU, A42174)—an irregularly branched form. C. Investigator Strait, S. Aust., 43 m deep (Watson, 27.i.1971; ADU, A38143)—distichously branched form. D. Branch showing arrangement of ramelli (Pt Denison, W. Aust. Kraft, 14.xii.1971; ADU, A41730). E. Ramelli with tetrasporangia (Vivonne Bay, Kangaroo I., S. Aust. Womersley, 30.i.1956; ADU, A20170).



in diameter and tapering fairly abruptly to a point, (70–)100–150  $\mu\text{m}$  thick, cells about 1(–1.1) times as long as broad. Ramelli with 16–20 nodal cells, each cutting off 1–2 cells (which often divide again) on both sides (anteriorly first), producing a nodal band (2–)3–5 (–6) cells broad (Fig. 3J, K).

*Cystocarps* short-stalked, irregularly globular to bilobed, 400–600  $\mu\text{m}$  in diameter.

*Spermatangia* cover the lower (except basal) several segments of young ramelli of adventitious branchlets lying between older ramelli, forming male organs 120–200  $\mu\text{m}$  in diameter.

*Tetrasporangia* (Fig. 5E) sessile, 1–3 per cell, mostly on the upper (adaxial) side of the ramelli, subspherical, 50–90  $\mu\text{m}$  in diameter, tetrahedrally divided.

*Type locality*: Holdfast Bay, S. Aust. (F.v. Mueller).

*Type*: MEL, 45128.

*Distribution*: From Port Denison, W. Aust. to Gabo I., Vic. *S. dasyoides* usually occurs on rough-water coasts from low tide level to depths of 33 m. Deeper growing plants are usually more delicate than those growing in turbulent conditions.

The reproductive cells develop very similarly to those in *S. filamentosa* or *S. tasmanica*. Female axes correspond well with that illustrated (Fig. 3G) for *S. tasmanica*, having alternating sterile and procarpic segments, with the latter comprising a 4-celled carpogonial branch on the supporting cell and usually two other periaxial cells. The mature cystocarp encloses two or three discrete carposporophyte lobes and the pericarp is relatively firm at its periphery.

*S. dasyoides* is characterised by its robust, opposite and more or less decussate ramelli, with cells about as long as broad and nodal bands 3–5 cells broad, together with the largely distichous branching. Eight periaxial cells are formed in branches and soon become separated

by rhizoidal cells, thus forming both nodal and internodal rings of usually 16 cells, the bands being about equal in length.

The type of *S. dasyoides* (Fig. 5A) in MEL is typical of this species, previously known mainly as *S. opposita*, Sonder's hand-written label with the holotype gives the locality as "Adelaide", inland from Holdfast Bay. The type of *S. opposita* (in TCD) is from Preservation Harbour, on the south-west coast of the south island of New Zealand (Lyal, Jan. 1851), and agrees very well with the southern Australian plants. Adams (1972, p. 83) records *S. opposita* from several localities near Wellington, New Zealand, and although it is apparently not widely known in New Zealand, the specimens (e.g. CHR, 55775, from Patu-rangi, Nelson) agree well with Australian material. The type of *S. prolifera* Harvey, in TCD, is from Fremantle, Western Australia (Clifton), and is a plant with denuded branches bearing proliferous branchlets. *S. prolifera* represents older plants of *S. dasyoides*, where the thick axes and branches are probably remnants of the previous years' growth, from which numerous short branchlets have arisen proliferously. The structure of the ramelli is identical with that of *S. dasyoides*. Plants referred to *S. prolifera* are apparently not infrequent on the Western Australian coast, where younger and typical plants of *S. dasyoides* also occur.

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